LIFE CYCLES AND ALARY MORPHS OF SOME DUTCH *GERRIS* SPECIES (HETEROPTERA, GERRIDAE)

by

KARI VEPSÄLÄINEN

Department of Genetics, University of Helsinki, Finland

and

NICO NIESER

Laboratorium voor Zoölogische Oecologie en Taxonomie, Utrecht, The Netherlands
With two figures

ABSTRACT

Material of *Gerris* species was collected in the Netherlands during one summer, mainly of *G. odontogaster* (Zett.) and *G. lacustris* (L.), and less of *G. argentatus* Schumm. and *G. thoracicus* Schumm. Dutch populations are bivoltine like those in Central Europe.

G. odontogaster and *G. argentatus* are long-winged in the overwintering generation and alary dimorphic in the first new, midsummer generation. Non-diapause adults emerge during a period of one month, in mid July at the latest. The last overwintered adults die about mid July, non-diapause adults before the winter. Few eggs seem to be laid after mid August. The first new, overwintering diapause adults (macropters) emerge about 10 July, and a few younger instar larvae are still observed in September.

The life cycle of *G. lacustris* is similar to that of *G. odontogaster*, but short-winged adults also occur in the overwintering generation. There is a notable peak of short-winged imagos in midsummer and another peak in late summer. *G. thoracicus* is virtually long-winged throughout the year.

Evidence on colonization flights of midsummer non-diapause *G. lacustris* and *G. thoracicus* is given.

INTRODUCTION

Andersen (1973), Vepsäläinen (1971, 1974a, 1974b) and Vepsäläinen & Krajewski (1974) have shown regularities in the relationship between the life cycles and alary polymorphism of European *Gerris* species (see also Järvinen, 1976).

1) *Odontogaster* type populations are univoltine and long-winged in northernmost Europe, and multivoltine (mostly bivoltine) and dimorphic over the main range of the species. Diapause is determined by shortening day lengths at the first four larval instars. Hence adults which have moulted after mid July do not reproduce before the following spring. In northern Europe immediately reproducing (non-diapause) adults are short-winged, while diapausing adults are long-winged. In more southern populations the non-diapause group includes both short and long-winged individuals. Overwintering adults are long-winged.

2) *Lacustris* type populations are univoltine in northernmost Europe, and

bivoltine over the main range of the species. The populations are usually polymorphic through the year, although morph frequencies fluctuate. Diapause determination is as in *odontogaster* type populations. In northern bivoltine populations immediately reproducing adults are mainly short-winged; in southern populations both short and long-winged non-diapause individuals are found.

3) *Rufoscutellatus* and *najas* type populations are usually univoltine, and monomorphically long-winged or wingless, respectively.

The above grouping is a simplification of the highly varying life cycles in Finnish, Danish, Polish and Hungarian *Gerris* populations. For instance, the cycle of *G. thoracicus* in southernmost Finland is of the *odontogaster* type but Hungarian populations are, almost without exception, long-winged (Vepsäläinen, 1974a, 1974b). Moreover, dimorphic *G. najas* De Geer populations are also known (Poisson, 1957; Krajewski, 1969).

G. odontogaster and *G. lacustris* are distributed from northern Europe to the Balkans, *G. argentatus* and *G. thoracicus* reach northern Africa (for a survey of distributions, see Vepsäläinen, 1973). Diapause is thought to be an adaptation to adverse conditions, i.e. in winter, at least in most parts of Europe. Indeed, even in Faro, the extreme south of Portugal, the conditions in December are not favourable for larvae to reach adulthood. This is due to low food supply and low temperature. On the other hand, the autumn temperatures until November are comparable to cool summer days in the Netherlands and Denmark. So for southern populations a strategy with a longer reproductive season than in northern Europe could be possible. This could apply even to Dutch populations compared with Finnish, as in the Netherlands September is still quite warm, while in Finland it is often too cold for *Gerris* development. As in the northern hemisphere the days begin to shorten after summer solstice, about 22 June, diapause is determined all over the species ranges at approximately the same time. Therefore the mechanism of diapause determination may seem non-adaptive.

The purpose of the present work is to study the life cycles of Atlantic populations to reveal possible differences in the diapause reaction between these and northern and southern continental populations (Finland, Poland, Hungary). Simultaneously we report the alary morph frequencies, as the conditions of ponds and other small waters which are the main habitats of the *Gerris* species investigated may, on the average, be more stable and predictable in Atlantic than in continental climates. As a consequence Atlantic populations could maintain a higher frequency of midsummer short-winged adults than continental populations. The following are our results based on specimens collected in the Netherlands during 1974.

Sites studied

The study area (ca. 200 km²) is located in the northern part of the Veluwe, prov. of Gelderland, with the village of Elspeet (52°17′N, 5°47′E) in its centre. The landscape is dominated by some rows of sandy hills formed by pleistocenic ice, one running approximately north—south from Nunspeet to Garderen. Most of our

sites are at the foot of these hills. Northwest of Heerde there is another chain of such hills, the Woldberg.

Most of the area has been planted with coniferous trees, but there are still a number of heathlands (e.g. the Speulderveld) and local stands of deciduous trees (e.g. near Nunspeet) left.

Except for those on the Speulderveld, the sampled sites are quite isolated, lying in small clearings in woods. With each locality description distances to nearest sites sampled are given. All these aquatic habitats were isolated from each other by land.

Our collecting sites are a subset of aquatic habitats of the Veluwe selected for zooplankton and later *Nepomorpha* studies, and supplemented with a collection of Speulderveld habitats. They were chosen in such a way that a maximal range of local *Gerris* habitats could be sampled. The following localities were included:

N1, Nunspeet, Waskolk, about 1500 m², surrounded by woods, isolated. Semi-aquatic vegetation (*Carex, Eleocharis, Juncus effusus, Glyceria* and *Sparganium*) at edges, from where most Gerridae were collected. Bottom: sand with a thin layer of plant debris, depth about 1 m. Used as a swimming pool during summer. Distance to N2, 4 km.

N2, Nunspeet, Ossenkolk, about 1000 m², surrounded by woods, isolated. Vegetation at edges *Eriophorum, Juncus bulbosus* and *Sphagnum*; pond filled with vegetation, mainly *Eleocharis, Juncus bulbosus, Sphagnum* and *Utricularia*. Bottom: sand with a thin layer of plant debris, depth for the greater part about 50 cm. Distance to N1, 4 km.

N3, Ermelo, Speulderveld, *Carex rostrata* pool, about 100 m², in open heath, bordered by *Molinia*, with *Carex rostrata* growing in the greater part of the pool. Bottom with a thick layer of plant debris, depth of free water 10-50 cm. Distance to N7-15, 20-300 m.

N4, Garderen, Watergraafsmeertje, about 2500 m², surrounded by woods, isolated. *Juncus effusus* and *Molinia* at edges; pond for the greater part filled with vegetation, mainly *Juncus bulbosus, Eleocharis* (*multicaulis*), *Ranunculus* and *Scirpus*. Bottom: sand with a thin layer of plant debris, depth for the greater part about 20 cm. Distance to N3, 7-15, 6 km.

N5, Heerde, pond at Buitenzorg, about 500 m², surrounded by woods, isolated. Edges: sand and dry *Sphagnum*. For the greater part filled with vegetation, mainly *Sphagnum*. Bottom: sand with plant debris, depth about 50 cm. Distance to N6, 3 km.

N6, Heerde, Kikkersgat, about 1000 m², surrounded by woods, isolated. Edges with *Juncus bulbosus, Molinia, Rhynchospora, Scirpus* and *Sphagnum*; pond for the greater part filled with *Eleocharis multicaulis, Juncus bulbosus* and *Sphagnum*. Bottom with a thick layer of plant debris, depth about 50 cm. Distance to N5, 3 km.

N7-10, Ermelo, Speulderveld, the four pits, 2 to 10 m², on open heath, separated from each other by narrow dams, no water connections. Edges with *Calluna* and *Molinia*, pits partly filled with *Juncus bulbosus* and overhanging withered *Molinia*. Bottom: loamy soil with some plant debris, depth 5-80 cm. Distance to N3. N11-15, 20-300 m. The population of each pit: NE = N7, SE = N8, NW = N9, and SW = N10, has been studied separately.

N11, Ermelo, Speulderveld, *Potamogeton* pit, 40 m², edges with *Calluna*, pit for the greater part filled with *Potamogeton natans*. Bottom: loamy soil with plant debris, depth 10-100 cm. Distance to N3, N7-15, 20-250 m.

N12, Ermelo, Speulderveld, *Utricularia* pit, 5 m², on open heath, edges and bottom open sand with plant debris, a few *Utricularia minor* in the pit. Depth 5-25 cm. Distance to N3, N7-15, 10-250 m.

N13, Ermelo, Speulderveld, *Juncus articulatus* pool, 20 m², on open heath, edges with *Calluna* and *Juncus articulatus*, pool for the greater part filled with *Juncus bulbosus*. Bottom: sand with plant debris, depth about 20 cm but on 26.VI. it was without water, the bottom still wet; it is not known how many days the habitat was dry. Distance to N3, N7-15, 30-200 m.

N14, Ermelo, Speulderveld, *Salix* pond, 60 m², surrounded by *Salix* shrubs and some *Typha*; pond for the greater part filled with *Potamogeton natans* and some *Juncus bulbosus*. Bottom: loamy soil with plant debris, depth about 1 m. Distance to N3, N7-15, 15-300 m.

N15, Ermelo, Speulderveld, *Typha* pond, about 200 m², Gerridae collected in a corner overgrown with *Typha,* about 20 m². Bottom: sand with much plant debris (mainly from *Typha*), depth about 20 cm. Distance to N3, N7-14, 15-300 m.

METHODS

The 15 populations were studied, and the larger populations partially collected, every second week from 16 May to 4 September 1974, N1-6 already on 16-19 April. Predominantly adults were collected, but larvae of the fourth and fifth instars were also taken to confirm reproduction. Occasionally younger larvae were included. During sampling the sites were checked for the occurrence of first and second instar larvae to estimate when the last eggs were laid. Unfortunately, samples were not taken after 4 September when egg-laying perhaps still continued on some of the sites.

Adults were classified according to wing length (short wings or wingless as against long wings). Notes were made on age (on basis of hardening and pigmentation grade of the chitin), colour of the female venter, stage of maturation (ovarian and testis), presence of adipose tissue, pigmentation of the mesoalinotum, and developmental stage of indirect flight muscles. When this information is combined, it is possible to make a reliable study of the life cycles. Details and reasons for the classification outlined here are given by Andersen (1973) and Vepsäläinen (1974a, 1974b).

Habitat classification

The sites mentioned above were grouped for habitat features according to Vepsäläinen (1973) and showed little diversity (table 1). Shore vegetation was either sparse or moderately dense, the water surface was totally or moderately exposed to sunshine, and all ponds were stagnant and in late May over 10 cm deep. Plant coverage on water surface was mostly moderately to very dense, and showed in five cases a temporal change from scarce or moderate to dense. Two times the succession was reversed.

One site was classified as permanent (risk of drying up negligible), seven as semi-permanent (risk of drying up small), and seven as temporary (likely to dry up during exceptionally prolonged hot periods, i.e. at least once in some 50 years). In one semi-permanent and four temporary ponds depth of water had decreased under 10 cm by 26 June. One site (N13) was dry on 26 June but again contained water during the visit on 10 July.

RESULTS

Species numbers and habitats

Codes of each collecting site with habitat and species data are summarised in table 1. The number of species (apart from *G. rufoscutellatus*) per site varies between two and four (table 2). Permanent and semipermanent habitats (combined) tend to harbour more species than temporary ones (P=.025, one-tailed

Table 1. Sites studied, their habitat classification (see Vepsäläinen, 1973) and the recorded species. For the first three categories 1 means none or little, 2 = moderate, 3 = much. For permanency, 3 means temporary (* dry on 26 June), for water movement 1 = stagnant, and for depth 2 = at least 10 cm and 1 = less than 10 cm. If two habitat classifications are given, the first refers to early summer (usually 30 May) and the other to midsummer (usually 26 June; in parentheses). Recorded species are shown with +, not recorded with —; the first sign refers to the adults, the second one to the fourth and fifth instar larvae.

Site code	Shore veget.	Exposition of the site	Plant coverage on water surface	Perman- ency	Water movem.	Water depth	presence of species					
							la	od	ar	th	gi	ru
N 1	2	1	2	1	1	2	+	+	+	+	–	–
N 2	2	2	2(3)	2	1	2	+	+	+	+	–	–
N 3	2	1	2	2	1	2(1)	+	+	–	+	–	–
N 4	2	2	2(3)	2	1	2	+	+	+	+	–	–
N 5	1	2	2(3)	2	1	2	+	+	+	–	–	–
N 6	2(1)	1	1(3)	2	1	2	+	+	+	+	+	–
N 7	1	1	1(3)	3	1	2	+	–	–	–	–	–
N 8	1	1	2(1)	3	1	2(1)	+	–	–	–	–	–
N 9	1	1	2	3	1	2(1)	+	+	–	+	+	–
N10	1	1	2	3	1	2	+	–	–	+	–	+
N11	1	1	3	3	1	2(1)	+	+	–	+	–	–
N12	1	1	1(2)	3	1	2(1)	+	+	–	+	+	–
N13	2	1	1	3*	1	2*	+	–	–	+	+	–
N14	1	2	3	2	1	2	+	+	+	–	+	–
N15	2	1	2	2	1	2	–	+	+	–	–	–

Table 2. Number of species per habitat grouped for permanency.

Habitat	number of species	2	3	4
Permanent				1
Semi-permanent		1	1	5
Temporary		3	2	2

Mann-Whitney U-test; the null hypothesis is that the temporary habitat has the same distribution over species numbers as the more permanent habitat group).

Notably *G. argentatus* seems to prefer (semi-)permanent habitats, being absent only from one semi-permanent, but all temporary, habitats. *G. lacustris* seems to be indifferent to this habitat feature. For the remaining species the data are inconclusive.

Life cycles and alary morphs

We will try to give a general picture of wing length variation and life cycles in Dutch *Gerris*. Hence we have summed the information from all 15 localities in figs. 1 and 2. There are probably differences between populations (see Vepsäläinen, 1974b: 12-13) but our material is too scarce to reveal any.
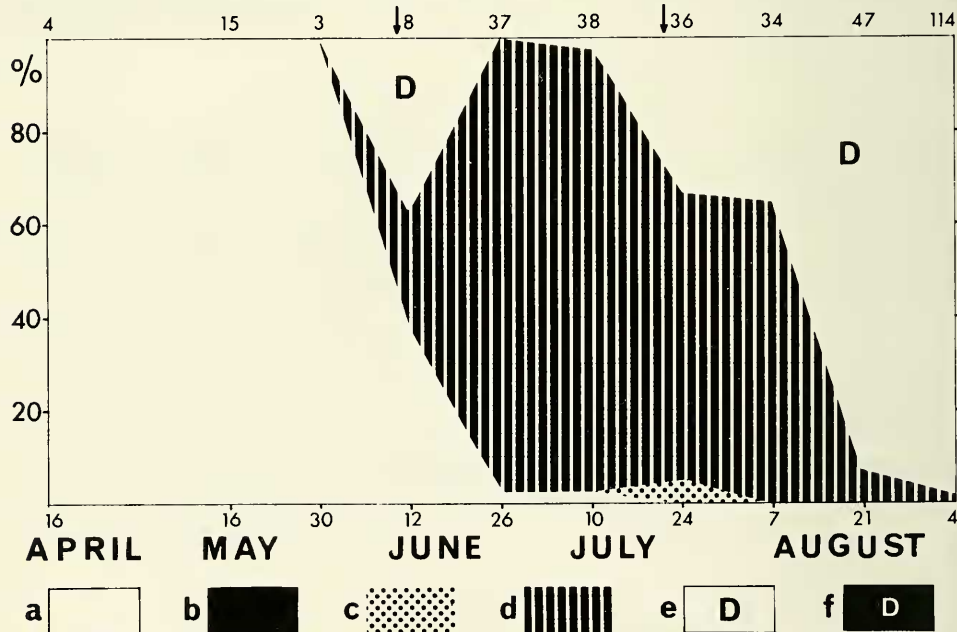

Fig. 1. Seasonal changes in the proportions of the different female forms of *Gerris odontogaster*. The numbers of females per sampling day are given above. The diagram is an approximation based on dissected material of 84.4% of the micropter and 44.1% of the macropter females. The arrows above indicate the first and last samples, respectively, where about newly emerged non-diapause females were found. a) hard chitin, dark venter, eggs or maturing oocytes, macropter; b) as *a* but short-winged; c) pale venter, eggs or maturing oocytes, macropter; d) as *c* but short-winged; e) dark venter, immature, macropter; f) as *e* but short-winged.

Gerris odontogaster

The overwintering population is long-winged. The first fifth instar larva was captured on 30 May. First short-winged adults were caught on 12 June and short-winged individuals dominated from late June to early August. The specimens in the late August and early September samples were almost all long-winged (fig. 1, table 3).

The short-winged adults are classified as micropters, wing length usually varying from 1 to 2 (see Vepsäläinen, 1974b, fig. 1). On 24 July, one male with wing length 3.5 (i.e. brachypterous) was collected (incompletely pigmented; age less than one week). The midsummer micropters are non-diapausing individuals whose gonads mature soon after the final moult. One to two weeks old micropterous females usually have full-sized eggs. Some non-diapause macropters emerge simultaneously with micropters. Both non-diapause female types are usually easy to distinguish from overwintered and diapause females by their pale venters in otherwise completely pigmented individuals. Males, however, are almost without exception dark below (for details, see Vepsäläinen, 1974a).

Diapause individuals with dark venter begin to emerge about 10 July, and gradually this group replaces other groups. The last two non-diapause females, which have been classified as semi-soft (refers to the hardening of the chitin), were captured on 24 July. As the hardening of the chitin may take over two weeks after the final moult, it can be estimated that the ecdysis has taken place about mid July. After 24 July all soft or semi-soft females checked for maturing oocytes have been in diapause. The mature, late summer females are older individuals, which have already laid most egg batches and die before the winter.

On 4 September no young larvae (first to third instars) were observed on eight

Table 3. Fraction of short winged specimens for males and females in *G. argentatus* (apters), *G. lacustris* (mainly brachypters) and *G. odontogaster* (micropters) with *s* (standard deviation in sample) and, between brackets, *n* (the number of specimens in sample) over all habitats on the various sampling days. Actually sampling took place on two consecutive days, of which the first is mentioned.

	G. argentatus sexes pooled		G. lacustris ♂		♀		G. odontogaster ♂		♀	
date										
16.IV	0	(5)	0.07±0.07	(14)	0.10±0.10	(10)	0	(11)	0	(4)
16.V.	0	(18)	0.06±0.04	(32)	0.10±0.05	(42)	0	(12)	0	(15)
30.V.	0	(3)	0.11±0.06	(28)	0.32±0.09	(28)	0	(1)	0	(3)
12.VI.	0	(5)	0.25±0.15	(8)	0	(10)	0	(4)	0.38±0.17	(8)
26.VI.	0.75±0.22	(4)	0.47±0.13	(15)	0.67±0.10	(24)	0.96±0.04	(23)	0.97±0.03	(37)
10.VII.	1	(12)	0 42±0.08	(36)	0.41±0.08	(44)	0.73±0.10	(22)	0.95±0.04	(38)
24.VII.	0.80±0.18	(5)	0.27±0.06	(49)	0.29±0.07	(49)	0.74±0.10	(19)	0.61±0.08	(36)
7.VIII.	0.39±0.14	(13)	0.12±0.04	(67)	0.15±0.05	(65)	0.64±0.13	(14)	0.65±0.08	(34)
21.VIII.	0	(11)	0.17±0.07	(30)	0.41±0.10	(27)	0.04±0.03	(47)	0.06±0.04	(47)
4.IX.	0	(29)	0.49±0.08	(39)	0.50±0.09	(32)	0.02±0.02	(65)	0.01±0.01	(114)

sites, and in seven populations they were very few or few. The species could not be identified in the field. On 21 August four populations had still "quite a number" of young larvae.

The one macropterous male checked for testis maturation on 7 August still had soft chitin (hence it was not over a week old) and well-developed testes. It is not known which proportion of late summer males has well developed testes nor whether they actually copulate in late summer.

Histolysing indirect flight muscles were already found on 16 April in over-wintered females with developing oocytes, and totally histolysed ones in females with eggs on 16 May. Micropters have undeveloped flight muscles, but non-diapause as well as diapause macropters develop indirect flight muscles in approximately two to three weeks in nature. It seems that an individual with the combination of characteristics — fully pigmented, semi-hard, mesoalinotum III or perhaps II (for the classes, see Andersen, 1973, fig. 10), and indirect flight muscle fibres with a diameter of 35-50 µm — is already capable of flight.

Adipose tissue was found in individuals with undeveloped gonads. Non-diapause individuals did not have adipose tissue; this was also the case with the micropterous female with eggs, collected on 4 September.

In the following we list some exceptions from the above life history picture. In the 12 June samples we found one semi-soft/semi-hard (hence not overwintered), fully pigmented, dark-ventered female with undeveloped oocytes, and one semi-soft, almost fully coloured female with dark venter and undeveloped oocytes (both macropterous). Usually the oocytes of new-generation females which develop in early summer are already well maturing in fifth larval instars (e.g. Andersen, 1973, fig. 7).

In the 10 July sample there was one semi-hard, completely pigmented, macropterous female with light venter but totally undeveloped oocytes (meso-alinotum II and diameter of indirect flight muscle fibres about 30 µm).

Collected on 26 June, there is one light-ventered micropterous female with abnormal intestine and no eggs, and on 10 July, one semi-soft, light-ventered micropterous female with contents of abdomen "rotten".

One micropterous male, collected on 24 July, had asymmetrical wings, one hemielytron being longer and deformed.

Sex ratio was female weighted (39.5% males, $n=554$, $P<.001$; .95 confidence limits for fraction of males .36-.44). The deviation is a sum effect of both midsummer micropters and late summer diapause macropters. (Heterogeneity $\chi^2_{(7)} = 13.60$, $.10<P<.05$; with the null hypothesis of even sex ratio in the samples. The heterogeneity of the whole material (early summer included) is statistically significant: $\chi^2_{(11)} = 24.32$, $P<.025$). Significant heterogeneity indicates a shift in sex ratio during the cycle.

Gerris argentatus

The number of specimens is small, 105 imagoes in all. The general picture is like that in *G. odontogaster* (table 3). The overwintering population is long-winged, the

midsummer one dimorphic. The short-winged individuals are mostly apterous but sometimes micropterous. On 10 July one newly emerged male with hemielytra 6 + and hind wings 4 + (brachypterous) was taken.

In this species also a few long-winged, non-diapause adults occur together with apters: one macropterous female on 7 August had completely hardened chitin, light venter and full-sized eggs.

Midsummer non-diapause females differ from diapause females by their more or less light venter. However, Dutch *G. argentatus* females are usually notably darker than the equivalent type in *G. odontogaster* (the former as the pattern *argentatus* D' and the latter as B' or C' *odontogaster* in fig. 3, Vepsäläinen, 1974a). No differences have been noticed in the ventral coloration between non-diapause short- and long-winged females.

The last overwintered adult (with strongly histolysed indirect flight muscles) was collected on 26 June. The first new generation apters were taken on the same day, and the first fifth instar larva on 12 June. No soft non-diapause individuals were collected after 10 July, and the first diapause macropters were not taken before 7 August. (On 24 July only five adults were captured.)

Indirect flight muscle histolysis was noted from 16 April onwards in overwintered individuals. In late summer, diapause imagoes had well-developed indirect flight muscles and voluminous adipose tissue.

The fraction of males was 50% (n = 105).

Gerris thoraćicus

In this species no definite evidence of alary dimorphism was obtained. The collected 61 imagoes were macropters with the exception of one male brachypter in the 10 July sample.

The Dutch population, like in the two previous species, is bivoltine (at least partially). The first fifth instar larva was captured on 12 June, and the first new, non-diapause imagoes (1 ♂ 3 ♀) on 26 June. The last overwintered specimen (1 ♂) was caught likewise on 26 June. The last young non-diapause imago was obtained on 10 July, and the first records of diapause individuals are from 24 July (two semi-hard young individuals, one of which had reached stage IV mesoalinotum coloration). The last female with eggs occurred on 21 August.

G. thoracicus differs from the previous two species in that both diapause and non-diapause individuals are nearly entirely dark below. The ventral coloration is therefore not indicative of a reproductive stage.

Another difference with the preceding species is evident: usually, histolysis of indirect flight muscles does not take place in overwintered *G. thoracicus*. In the last overwintered specimen (1 ♂ on 26 June) indirect flight muscles were still full-sized.

The one brachypterous male (semi-hard, totally pigmented, hemielytra 7.2, hind wings 5.2; called submacropter by many previous investigators) had well developed testes but undeveloped flight muscles.

The fraction of males was 46% (n = 61).

Gerris lacustris

This species has a more complicated life cycle as even the overwintering population is polymorphic. A notable peak of brachypters (the other morph in this species, medially short wings) occurs in midsummer. Later the relative frequency of brachypters declines to rise again in the early September sample. In late spring brachypter frequencies are at the lowest (fig. 2, table 3).

The high frequencies of brachypters in mid summer are explained by the fact that a higher proportion of the non-diapause imagoes are short-winged (fig. 2). The situation is analogous with *G. odontogaster* and *G. argentatus* which have a mid-summer short-winged, non-diapause group, except that *G. lacustris* populations also include overwintering brachypters.

The first fifth instar larva was captured on 12 June, and the first new, non-diapause adults (both brachypters and macropters) on 26 June. The last over-wintered imago (one brachypterous female) was caught on 10 July.

The last young, definitely non-diapause adult (a brachypterous female), incompletely pigmented and semi-soft, with the largest oocytes at least 860 µm, was captured on 10 July. However, still on 24 July one brachypterous female, soft and incompletely pigmented (signs of darkening venter could be traced), still had oocytes of 550 µm maximum length. Furthermore, on the same day one semi-soft and incompletely pigmented brachypterous female (with signs of dark venter) with maximal oocyte length of 480 µm was caught. These two oocyte measurements lay at the lower boundary of the class "maturing" of Andersen (1973: 500 µm) but

Fig. 2. Seasonal changes in the proportions of the different female forms of *Gerris lacustris*. Symbols as in fig. 1 but instead of dark (light) venter read dark (light) thoracic venter. The diagram is an approximation drawn on basis of 60.6% of the brachypter and 42.2% of the macropter females.
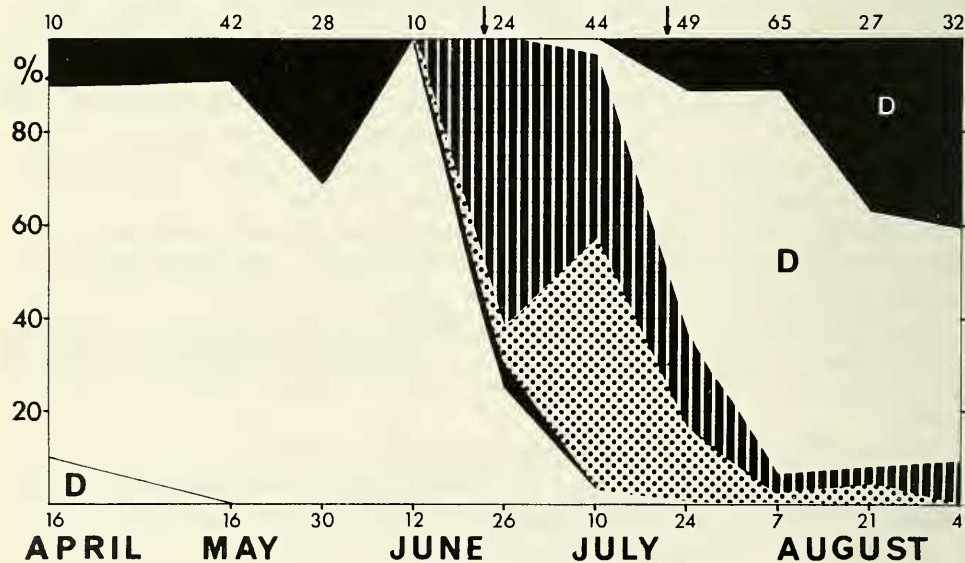
considerably exceed the 240 µm used by Vepsäläinen (1974a) in routine scrutiny. It is not clear whether these two females really were diapausing or not. The coloration of the thoracic venter indicates diapause (accordingly a later resorption of oocytes is to be expected). The colour of the venter is, however, only a good working guide, as in the same samples there is one semi-hard, ventrally dark (only sternites 6 and 7 medio-apically light) brachypterous female with eggs. In this case there could not be any question of an overwintered adult as the ventral coloration was still partially brown-black (a sign of ongoing pigmentation). Another puzzling individual is the macropterous female caught on 7 August, which was incompletely pigmented, semi-soft/semi-hard and had only one, 365 µm long oocyte in its otherwise undeveloped ovaries.

Thus it is clear that whether the females were classified as maturing by the criterium of minimum oocyte length of 240 µm or 500 µm, it is preferable to check for additional signs of diapause in border cases as well. The positive correlation between reproductive activities and poorly developed adipose tissue, and diapause and well-developed adipose tissue seems to hold true in individuals which have attained at least semi-hard chitin, but is poorly developed in soft and semi-soft imagoes, even if completely pigmented.

Non-diapause adults were still found in late August and early September, although the numbers were low. The first diapause imago occurred on 10 July, and on 24 July diapause imagoes dominated in the total material.

The positive relation between a light thoracic venter and a non-diapause state in *G. lacustris* is good in our Dutch material. Only one possible exception (above) was found. Moreover, at least four macropterous females were seen (on 24 July), in which the general impression was all-dark. A closer inspection revealed that in all these individuals the pattern of lighter non-diapause adults could be seen. The coloration was only more grey-brown than usually ("smoky"), but still contrasted against the black areas of the thoracic venter. The coloration was much the same as in the non-diapause type of *G. paludum* F. in fig. 3 by Vepsäläinen (1974a).

Brachypterous *G. lacustris* adults have undeveloped flight muscles. Diapause macropters develop functional muscles, which, after overwintering, are histolysed. In our Dutch material we already have macropterous females with histolysing muscles on 16 May. In mid summer, diapause imagoes seem to reach flight ability in about two weeks or shorter: two females collected on 24 July were semi-hard, totally pigmented, with mesoalinotum II and the diameter of indirect flight muscle fibres 30-50 µm and 32-45 µm, respectively.

Sex ratio of brachypters is perhaps female-weighted (43% males, n=174, P=.07); in macropters the male percentage is 51 (n=475).

Other species

Altogether 23 *G. gibbifer* Schumm. adults (10 ♂, 13 ♀) were collected, all macropters (one female with hemielytra 7.8 and hind wings 7.0-7.1). The first new generation adult was caught on 26 June; it was a semi-soft female with undeveloped oocytes. Oocyte maturation could not be detected in an already

semi-hard/hard female on 10 July. Thus the voltinism of Dutch *G. gibbifer* cannot be determined on the basis of our material.

Only two observations of overwintered *G. rufoscutellatus* Lat., probably the same female, were made: on 30 May, and 12 June, when its abdomen was swollen with eggs. No larvae were found.

Midsummer colonization flights

Usually little can be said about colonization flights without marking-recapture work. The temporary drying up of pond N13 (dry on 26 June, water on 10 July), however, gave some information.

On 26 June the bottom and the bordering vegetation were checked for *Gerris*: none were found. On 10 July one *G. thoracicus* macropterous male and one *G. lacustris* macropterous female (semi-hard, light thoracic venter, eggs; thus a midsummer, non-diapause adult) were collected. On 24 July another *G. thoracicus* macropterous male and *G. lacustris* macropterous female (semi-hard, light thoracic venter, eggs, totally pigmented mesoalinotum and well developed indirect flight muscles) were taken.

On 7 August two fifth instar larvae of *G. gibbifer* and three *G. thoracicus* females were netted. The *G. gibbifer* larvae may have developed from eggs which survived the drought, as on 30 May and 12 June there was a *G. gibbifer* female in the pond. Of the *G. thoracicus* females, two had eggs and the third was in diapause. As no *G. thoracicus* larvae were collected from N13, it is improbable that the adults had developed there.

Accordingly, colonization flights of mid summer reproducing *G. lacustris* and *G. thoracicus* do occur. Earlier straight evidence is rare. Fernando (1959) reports one immigrant *G. odontogaster* female which produced offspring. Here the female was fertilised before the migration, as perhaps, were some females of our immigrants to population N13. There seems to be a clear difference therefore in the stage of maturation between colonising overwintered and colonizing midsummer females, as spring migrants have undeveloped or very poorly maturing oocytes (Landin & Vepsäläinen, 1977).

Discussion

The life cycles and wing lengths of the studied *Gerris* species are by and large similar to those in Poland (Vepsäläinen & Krajewski, 1974) and Hungary (Vepsäläinen, 1974a). The Dutch populations differ, however, in these respects from more northern ones in Finland (see Vepsäläinen, 1974b). Admittedly, there are more non-diapause macropters in the mid-summer generation in Hungary (and, considering *G. lacustris*, also in Poland). This could reflect the higher degree of temporariness of more southern and continental pond habitats.

The diapause of Dutch *Gerris* seems to be fixed at about the same date, and presumably by the same mechanism, as that of Finnish, Polish and Hungarian populations (for a generalized model, see Vepsäläinen, 1974c: fig. 2).

In northern Europe early winter understandably favours diapause determination

by decremental changes of day length. On the average the potential reproductive season is longer and the risks of drying up of population sites are smaller in Atlantic climates than in continental ones at the same latitudes. Thus it could be assumed that in Dutch populations selection would operate towards a later termination of reproductive activities. This could be achieved in at least two ways: by later onset of diapause and/or longer life span of the midsummer, non-diapause adults.

Usually the diapause of insects is determined by the absolute lenghts of daily illumination period (Danilevskii, 1965) but in *Gerris* the change of length is critical: shortening day lengths determine the diapause. Thus it is not easy to postpone the onset in diapause in *Gerris*. The associated genetic changes would have to be radical, and would be possible only in effectively isolated populations under strong selective pressure. The Dutch populations in this respect are not submitted to strong natural selection and are insufficiently isolated. From the degree of temporariness of our study ponds it can be presumed that gene flow between local *Gerris* populations is notable, which is in agreement with the general views on migration strategies of the denizens of more or less temporary habitats (e.g. Southwood, 1962; Dingle, 1974; Vepsäläinen, 1974b). Even long range flights are known (Leston, 1956). These tend to swamp the effects of local selection pressures. Moreover, a recent simulation study on *Gerris* populations (Järvinen & Vepsäläinen, unpublished) showed that even in the absence of imminent threat of unfavourable conditions it may sometimes (e.g. in habitats of low productivity) be advantageous to limit the number of successive generations.

The strategy to postpone the end of reproductive activities by cutting down the mortality of the midsummer non-diapause adults is likely to work in *Gerris*. Unfortunately we lack Dutch data on last first-instar larvae in autumn. Consequently, nothing can be said of the approximate last day of egg-laying of Dutch *Gerris*. Here would be an important field of study: to work out the length of the reproductive season in terms of last egg-laying dates of *Gerris* species in different parts and climates of the western Palaearctic. The theoretical value of such a study is evident, as the onset of diapause seems to occur about the same date everywhere irrespective of the widely differing lengths of the potential reproductive season.

Another point of discussion comes from our observation of two completely pigmented new-generation *G. odontogaster* females (semi-hard and semi-soft) with dark venter and undeveloped oocytes, captured on 12 June. The observed features together are a reliable sign of diapause. Vepsäläinen (1974d) obtained such laboratory offspring of Finnish *G. odontogaster* which were reared in short, lengthening illumination. The applied laboratory days were shorter than Finnish late instar larvae can meet in nature in early summer. Such females are expected to be very rare in natural populations, as the selection pressures are heavy against diapause behaviour in early summer. It cannot, however, be ruled out that oocyte maturation both in the Finnish laboratory reared and the Dutch females was only retarded and would have started later in somewhat longer days, producing exceptionally new-generation females with eggs, though with dark venter. Such individuals have very rarely been observed (e.g. Vepsäläinen & Krajewski, 1974, in

G. lacustris). We presume that retarded maturation instead of real diapause is the more likely explanation in some individuals which develop in short, lengthening days — i.e. exceptionally early in summer — in nature.

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